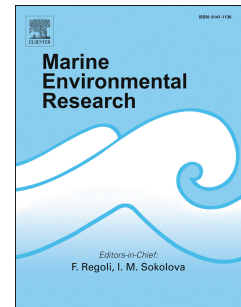


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# Effects of environmental change and early-life stochasticity on Pacific bluefin tuna population growth

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## Highlights

- We developed a novel tool that relates environmental change to population dynamics.
- We used the new tool to analyze Pacific bluefin tuna (PBT) population growth.
- We found that PBT population experiences a positive growth rate.
- Surprisingly, stochasticity in early life survival speeds up population growth.
- PBT fishing is tolerable if environment supports fast enough maturation ( $< 9$  y/o).

## Abstract

Species conservation and fisheries management require approaches that relate environmental conditions to population-level dynamics, especially because environmental conditions shift due to climate change. We combined an individual-level physiological model and a conceptually simple matrix population model to develop a novel tool that relates environmental change to population dynamics, and used this tool to analyze effects of environmental changes and early-life stochasticity on Pacific bluefin tuna (PBT) population growth. We found that (i) currently, PBT population experiences a positive growth rate, (ii) somewhat surprisingly, stochasticity in early life survival increases this growth rate, (iii) sexual maturation age strongly depends on food and temperature, (iv) current fishing pressure, though high, is tolerable as long as the environment is such that PBT mature in less than 9 years of age (maturation age of up to 10 is possible in some environments), (v) PBT population growth rate is much more susceptible to changes in juvenile survival than changes in total reproductive output or adult survival. These results suggest that, to be effective, fishing regulations need to (i) focus on smaller tuna (i.e., juveniles and young adults), and (ii) mitigate adverse effects of climate change by taking into the account how future environments may affect the population growth.

## Introduction

Changes in the oceanic environment, particularly those induced by climate change, are predicted to have a large socioeconomic impact through their effects on commercial fisheries and food security (Allison et al., 2009; Barange et al., 2014; Bell et al., 2013; King et al., 2015). Fisheries, even if managed properly, are expected to be impacted by effects of climate change on various ecological processes (Koenigstein et al., 2016; Stenseth et al., 2002). For example, ocean warming, acidification, and oxygen depletion are likely to affect ontogeny and foraging alike, and consequently population dynamics, community structure, and finally ecosystem function (Koenigstein et al., 2016). Understanding and predicting the potential impact of novel environments on key ecological or commercial species is thus of paramount importance.

Pacific bluefin tuna (*Thunnus orientalis*; hereafter PBT) has an enormous market potential (Naylor and Burke, 2005). Presently, however, PBT is considered to be an overexploited species (Collette et al., 2011; Juan-Jordá et al., 2011) whose spawning biomass—according to the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC)—has been decimated to a few percentage points relative to its pristine state. Following such a dire estimate, the Western and Central Pacific Fisheries Commission (WCPFC) adopted a rebuilding plan for the PBT stock (e.g., Nakatsuka et al. (2017)) which considers the uncertainty in recruitment (Ishida et al., 2017), but falls short of accounting for the potential effects of a changing oceanic environment on this stock. We set out to showcase a modeling framework for estimating PBT population growth in the face of both the uncertainty in recruitment and the environmental change. This framework is consistent with the principles of physiological energetics (Jusup and Matsuda, 2015;

Jusup et al., 2017a; Kooijman, 2010; Nisbet et al., 2000, 2012; Sousa et al., 2008, 2010, 2006), prioritizes the ecological relevance of size over age (De Roos and Persson, 2001, 2002; Pauly, 1980; Persson and De Roos, 2006; Werner and Gilliam, 1984), and generates the population-level effects as an emergent property of the individual-level interactions with the environment (Ananthasubramaniam et al., 2015; De Roos and Persson, 2001; Martin et al., 2012; Nisbet et al., 2000; Persson and de Roos, 2013; Smallegange et al., 2017).

Ours is not the first approach to consider the influence of environmental change on population dynamics. Previous models assumed that recruitment or population growth rates change as the environment changes (Hilborn et al., 1992; Post and Stenseth, 1999; Stenseth et al., 2002), but relied on empirical assumptions to relate changes in the environment to population-level effects (e.g., recruitment and population growth rate), thus effectively skipping the level of the individual. This becomes a problem when multiple effects need to be combined in the same model, and no multi-variate data linking all possible environments to population-level response exist. Mechanistic models, by contrast, link all levels of biological organization, from the state of the environment (*e*-state) to the condition of individuals (*i*-state), from which then population growth (*p*-state) emerges as a matter of bookkeeping of all individual-level states (Persson and De Roos, 2006; Yokoi et al., 2017). For example, growth rates increase and maturation times shorten if the environment is favorable (Jusup et al., 2014, 2011). Faster growth and maturation, in turn, allow fish to race through their most vulnerable—larval and early juvenile—life stages (Werner and Gilliam, 1984), thus potentially reducing high mortalities associated with those stages. Changes in food abundance could affect batch fecundity as well (Kjesbu et al., 1998). Once all of these causal chains are linked into a model, the effects of combinations of environmental changes can be directly calculated by

running the complete mechanistically built model.

Early-life stochasticity in recruitment is also a major factor affecting fish life histories and population dynamics. In contrast to terrestrial animals which exhibit a relatively clear relationship between the number of reproductive adults and the number of offspring, the relationship between spawning biomass and recruitment of pelagic fish has proven much more elusive (Lowerre-Barbieri et al., 2017; Simon et al., 2012). Multiple mechanisms are thought to modulate successful recruitment, including the environmental change itself (Daewel et al., 2011; Hedgecock and Pudovkin, 2011). In the case of PBT in particular, a lower surrounding seawater temperature decreases larval growth rates, which in turn is likely to have a negative impact on larval survival (Kimura et al., 2010). PBT larvae is also critically dependent on favorable ocean currents to secure a low energetic cost of transport to known nursery areas in the Japanese coastal waters (Kitagawa et al., 2010). Generally, early-life mortality of fish exhibits strong density dependence (Hazlerigg et al., 2012), with PBT larvae being especially notorious for increased cannibalism in high-density conditions (Sawada et al., 2005). Despite all these complications, estimates of early-life mortality do exist for Atlantic bluefin tuna (Simon et al., 2012), which is PBT's close relative inhabiting the Atlantic Ocean with spawning grounds in the Mediterranean Sea, or the Gulf of Mexico (Rooker et al., 2007).

Hereafter, the Methods section presents a conceptual outline of the modeling techniques used to couple individual- and population-level models. Based on a reviewer's recommendation, we displaced a self-contained, technical description of employed modeling techniques to the Supplementary Methods. The Results section details the effects of environmental change and early-life

stochasticity on PBT population growth and identifies which vital rates critically affect the corresponding growth rate. Finally, the Discussion section considers the implications of the results for PBT fishery management, outlines our concerns regarding the coupled individual-level and population-level modeling framework, and lists opportunities for future developments, especially applications in conjunction with archival tag data.

## Material and methods

To develop a framework for modeling PBT population growth which is capable of accounting for both environmental change and early-life stochasticity, we coupled (i) a calibrated and validated, individual-level model of PBT ontogeny (Jusup et al., 2014, 2011) built on the principles of physiological energetics (Jusup et al., 2017a; Nisbet et al., 2000; Sousa et al., 2008, 2010) and (ii) a matrix population dynamics model for bookkeeping the population renewal through recruitment relative to population losses through natural and fishing mortalities (Fig. 1). Physiological energetics model accounts for energy acquisition and consumption of an individual fish in order to estimate the potential for growth, maturation, and reproduction by applying the conservation laws of mass and energy (Jusup and Matsuda, 2015; Nisbet et al., 2012). Both energy acquisition and consumption depend on the prevailing environmental conditions, implying that the ontogeny of the modeled fish changes in response to changes in the the environment.

Once the individual-level model's parameters are calibrated and outputs validated, there are multiple ways to progress from individual ontogeny to the corresponding population dynamics. Individual-based modeling (IBM) is a direct, but extremely computationally intensive approach, in

which a large number of individuals are modeled until death while keeping track of their offspring (Martin et al., 2012; Schindler et al., 2002). Alternative approaches include integration with partial differential equations (De Roos and Persson, 2001), projection matrices (Klanjscek et al., 2006), and integral equations (Smallegange et al., 2017). Here, we opted for integration with matrix population models (hereafter MPMs) due to their conceptual clarity (Caswell, 2001), long tradition in fishery science (DeAngelis et al., 1980), and a relatively easy implementation with modern-day computational power. Unlike IBMs, MPMs do not need actual simulations to yield population-level information; for example, the dominant eigenvalue of the projection matrix of an MPM is an indicator of population growth and, as such, a staple of conservation ecology (Caswell, 2001). MPMs furthermore come with a well-defined concept of elasticity which allows us to evaluate the percentage change in population growth caused by the percentage change in vital rates, i.e., fecundity or survival (De Kroon et al., 1986, 2000). Another reason for choosing MPMs is that stochasticity in life-history traits, such as uncertain recruitment, is readily accounted for (Åberg et al., 2009; Boyce et al., 2006; Tuljapurkar et al., 2009).

**In summary,** we devised a modeling framework comprised of two model types. A foundation is provided by an individual-level model based on the principles of physiological energetics (Jusup and Matsuda, 2015; Jusup et al., 2017a; Kooijman, 2010; Nisbet et al., 2000, 2012; Sousa et al., 2008, 2010, 2006) and capable of predicting PBT growth, maturation, and reproduction as a function of the state of the environment (Jusup et al., 2014, 2011; Jusup and Matsuda, 2015). Outputs from this individual-level model are fed to a population-level model based on projection matrices (Klanjscek et al., 2006). Because the predictions of growth, maturation, and reproduction were handled at the individual level, only assumptions on fish survival were required to complete



the parameters necessary for the population-level model. The overall purpose of such a coupled framework was to achieve sufficient flexibility to account for the effects of varying food and temperature in the environment, as well as for the effects of stochasticity in the early-life survival of PBT on the population growth rate. An interested reader can find a self-contained, technical description of the employed models in the Supplementary Methods, which includes all information (e.g., notation, equations, parameter values, etc.) needed to recreate the results that follow.

## Results

Growth, maturation, and reproduction of PBT strongly depend on the prevailing environmental conditions. For example, if food abundance is sufficient for PBT to maintain ingestion at 90 % of the maximum for a given size, which approximately corresponds to the current food abundance in the wild (Jusup et al., 2011), the tuna are able to grow to about 250 cm fork length, but the rate of growth is dependent on the experienced seawater temperature (Fig. 2A). At 19 °C, which again corresponds to the average temperature in the wild (Jusup et al., 2011), fish reach the approximate size of sexual maturity of 150 cm fork length at the age of 5.1 years, whereas at 25 °C, the same size is reached at the age of 3.6 years. If food abundance drops and ingestion is maintained at 80 % of the maximum, PBT are barely able to grow above the size of sexual maturity (Fig. 2A), and the time to do so may take anywhere between 8.8 years at 25 °C to 12.5 years at 19 °C. Empirical evidence that the growth of PBT is strongly dependent on temperature is found in aquaculture data directly (Masuma et al., 2008), while inferring the dependence of growth and maturation on food abundance is somewhat more convoluted, but possible (Jusup et al., 2014). Having calculated growth, maturation, and reproduction, to proceed to population-level calculations, only survival

probability as a function of age remains to be specified.

Hazard rates in fish typically depend on size, but the population dynamics model requires survival as a function of age. The fishing hazard depends on size because the fishing gear itself selects for size rather than age (Millar, 1992), and natural hazard has long been associated with size (Werner and Gilliam, 1984). Both of these hazards as functions of size, and the resulting combined hazard rate, are given in Fig. 2B. The combined hazard rate-at-length is then transformed to the survival probability-to-age (Fig. 2C,D). Note that, because length-at-age depends on environmental conditions, so does the survival. For example, survival probability drops below 1 % at the age of 5.1 years (Fig. 2C) under the current fishing effort and conditions experienced in the wild (ingestion at 90 %, temperature of 19 °C). The same survival probability of 1 % would be reached at the age of 3.1 years if ingestion decreased to 80 % (Fig. 2D).

Having established that growth, maturation, reproduction, and even survival as a function of age depend on environmental conditions, we could calculate environmental effects on PBT population growth. Here, we assumed that the examined ranges of food abundance (80–98 % of the maximum ingestion for a given size) and seawater temperature (15–30 °C) are within the tolerance ranges of PBT.

The results of the population dynamics model show a considerable slowdown of population growth with decreasing food abundance and temperature (Fig. 3A). Overlying this with the age to sexual maturation, we find that the deterministic population growth rate is positive, i.e.,  $\lambda_{det} > 1$ , as long as environmental conditions stay sufficiently favorable for PBT to mature by the age of 6–7 years old. Result  $\lambda_{det} > 1$  holds in spite of the current high fishing effort, implying that the

conditions experienced in the wild—ingestion at 90 % and temperature of 19 °C—support positive PBT population growth (Fig. 3A), at least in the limit of a low population density. But, if population growth is positive, why did the biomass of temperate tuna reportedly decrease by 80.2 % from 1954 to 2006 (Juan-Jordá et al., 2011)?

Keeping in mind that  $\lambda_{det}$  is a deterministic measure valid at a low population density, we started investigating the question of population decline by acknowledging that considerable stochasticity in the early-life survival of bluefin tunas (Simon et al., 2012) is a potential culprit. We therefore replaced the deterministic population growth rate with its stochastic counterpart. Surprisingly, the stochastic form of the model shows that stochastic PBT population growth remains positive, i.e.,  $\lambda_s > 1$ , as long as these fish sexually mature by the age of 9–10 years old (Fig. 3B).

In fact, given the same environmental conditions, the stochastic population growth rate always exceeds the deterministic one, i.e.,  $\lambda_s > \lambda_{det}$ . This last inequality, though surprising at first, is a consequence of a convex, non-linear relationship between early-life mortality,  $M_0$  (Fig. 3C), and the deterministic population growth rate,  $\lambda_{det}$  (Fig. 3D). Namely,  $\lambda_{det}$  is simply a population growth rate calculated with the average value of early-life mortality,  $\overline{M}_0$ , whereas  $\lambda_s$  is the average of population growth rates calculated with various values of  $M_0$  drawn from an empirical distribution (Simon et al., 2012). In such situations, Jensen's inequality dictates that  $\lambda_{det} = \lambda(\overline{M}_0) < \overline{\lambda(M_0)} = \lambda_s$  as long as function  $\lambda = \lambda(M_0)$  is a convex one, as is the case here. It is important in this context that  $\lambda_s > 1$  over a broad range of environmental conditions implies a remarkable robustness of the wild PBT stock, at least at a low population density. At the same time, stochasticity precludes any guarantee that the actual population growth rate is positive in any given year, meaning that

the risk of substantially depleting the wild PBT stock is very high when the periods of continued poor recruitment coincide with extreme fishing pressure. This partly answers the above-posed question about the decrease of temperate tuna biomass. For a full answer, it is critical to acknowledge the effects of “cohort resonance” (Bjørnstad et al., 2004) by which stochastic recruitment as a high-frequency (i.e., yearly) phenomenon, conspires with age-structured interactions to induce low-frequency (i.e., decadal) cycles in abundance. Such cycles do not constitute trends, but due to their persistence may carry considerable risks for what otherwise would be a thriving population.

To understand how vital rates (fecundity and survival) affect PBT population growth, we estimated stochastic elasticities, defined as percentage changes in the stochastic population growth rate arising from 1 % changes in the underlying vital rates. Our interest here was threefold. First, the sum of fecundity elasticities (Fig. 4A) isolates environmental effects on population growth from anthropogenic effects because the reproductive rate of an individual PBT (i.e., fecundity) cannot be directly affected by human actions. Second, the sum of juvenile survival elasticities (Fig. 4B) reflects environmental and human effects on population growth due to the interplay between ontogenetic development, natural mortality, and fishing mortality. Finally, the sum of adult survival elasticities (not shown because elasticities sum to unity) largely isolates human effects on population growth caused by fishing mortality. We find that the sum of fecundity elasticities is  $<20\%$ , and the sum of juvenile survival elasticities is  $>50\%$  in almost all environments. Only in the most favorable environments these values become comparable at approximately  $35\%$ . This means that, in most environments, population growth rate responds more to changes in juvenile survival than to changes in fecundity and adult survival combined. Therefore, fishing policies aimed at PBT juveniles may have a large impact on population growth because such policies would affect total

juvenile survival, whereas a carefully formulated fishing policy aimed at PBT adults would have a considerably smaller impact.

To see effects of a policy that focuses on juveniles and young adults, we examined more closely stochastic elasticities under low and high food abundance. In the former case (when ingestion is at 80 % of the maximum), we find that the elasticity of the total fecundity is low due to a slowed-down ontogeny. Changes in survival, especially that of juveniles, contribute the most to changes in population growth (Fig. 5A, B). The effect of temperature on stochastic elasticities is only marginal, but the age at which the total adult survival elasticity falls to <10 % may differ substantially, e.g., 26 years old at 19 °C and 18 years old at 25 °C (cf. panels A and B in Fig. 5).

When food abundance is close to what wild PBT experience today (i.e., ingestion at 90 % of maximum), faster ontogeny somewhat increases the total fecundity elasticity. Nonetheless, changes in survival, especially juvenile, still contribute the most to changes in population growth (Fig. 5C, D). The effect of temperature on stochastic elasticities is also more pronounced than at lower food abundance, but here the age at which the total adult survival elasticity falls to <10 % is relatively stable, 9 years old at 19 °C vs. 7 years old at 25 °C (cf. panels C and D in Fig. 5).

## Discussion

Herein, we evaluated the effects of environmental change and stochastic early-life survival on the Pacific bluefin tuna (PBT) population. To this end, we integrated a calibrated and validated, full life-cycle, dynamic energy budget model for PBT into a matrix population modeling (MPM) methodology, and calculated long-term population growth rate as a function of food abundance,

seawater temperature, and early survival stochasticity. Furthermore, we estimated stochastic elasticity of population growth to understand how changes in vital rates (fecundity and survival) affect the PBT population performance in different environments. We find that individual PBT grow faster in food-rich and warmer environments, which automatically implies that population growth rate is an increasing function of food abundance and seawater temperature (Fig. 3A, B). While these results are intuitive and thus perhaps not surprising, comparing the relative *importance* of food and temperature for the PBT population performance is much more informative. It turns out that positive population growth is possible only if food abundance is sufficient to maintain an ingestion rate above  $\approx 80\%$  of the maximum, because otherwise maturation is delayed irrespective of the prevailing temperature (Jusup et al., 2014). In contrast, given sufficient food abundance, PBT can maintain positive population growth at any temperature between  $15^{\circ}\text{C}$  and  $30^{\circ}\text{C}$ , which roughly corresponds to the temperature tolerance range for this species. We thus conclude that, although both environmental factors are important determinants of PBT population performance, it is food rather than temperature that plays an overall more critical role. Knowing that food plays a more critical role for PBT population performance helps us better understand findings on the relationship between the oceanic environment and the distribution of PBT.

For example, our findings that PBT should prioritize high food over high temperature could explain most of the features of PBT spatial distribution. Even though electronic tagging data suggest that PBT should choose habitats both for high primary productivity and high seawater temperature (Hazen et al., 2013), other data show that—as suggested by our model—PBT preferentially inhabit areas characterized by high primary productivity and spawning activity of their prey fish (subtropical and temperate waters of the North Pacific Ocean; e.g., Boustany et al. (2010)). Pre-

sumably for the same reasons, Atlantic bluefin tuna also prefer areas of high productivity (Walli et al., 2009). Because the tropical North Pacific has low productivity (Behrenfeld et al., 2006), we hypothesize that PBT are not likely to be found in this region despite potentially beneficial temperature effects. Another indicator of prioritizing food over temperature is the diving behavior of PBT, who are known to temporarily dive into cold water areas specifically for feeding (Kitagawa et al., 2004, 2007).

Early-life stochasticity increases the range of environmental conditions in which PBT population performs well (cf. panels A and B in Fig. 3). This result goes somewhat against the common wisdom that stochasticity decreases population growth rate (Boyce et al., 2006), although theoretical analyses do point to a positive relationship between stochasticity in early-life mortality and the recruitment probability in fish (Pitchford et al., 2005). Our results go beyond just recruitment probability and directly relate early-life stochasticity to higher population growth. To intuitively explain these results, we take into account that PBT are large-bodied fish who spawn huge numbers of eggs in a single reproductive season (Ashida et al., 2015; Okochi et al., 2016). How many of those eggs actually survive the larval stage is highly uncertain, leading to a situation in which there is almost no spawner-recruitment relationship for bluefin tuna (Simon et al., 2012). In a good year, therefore, even a relatively low spawning biomass may produce enough offspring for strong subsequent population growth. It would thus seem that the reproductive strategy of PBT and other related tuna species (high egg production and weak spawner-recruitment relationship) ensures some robustness against unfavorable environmental conditions and, by extension, against catastrophic exploitation.

Density dependence is one of the likely causes of early-life stochasticity. Namely, larval growth can slow down considerably when the density of larvae is high and the competition for available food is fierce (Hazlerigg et al., 2012). Given that the natural mortality of fish significantly depends on body length in general (Lorenzen, 1996), larval mortality is bound to increase in high density conditions. Furthermore, PBT larvae fall victim to cannibalism (Sawada et al., 2005), which also increases in high density conditions. The negative effects of density dependence can be compounded by natural fluctuations in food abundance and temperature. Larval ontogeny is thus affected by a complex interplay of stochastic factors the aftermath of which is that any relationship between the spawning stock and recruited juveniles essentially disappears. We believe that our modeling framework, armed with the appropriate extensions to account for hydrodynamics and primary production, is flexible enough to test some of these hypotheses. This is a potentially interesting direction for future research.

Another possibility for future research is to replace our working assumption of the average environmental conditions with one that accounts for regional differences. While the current assumption is justified by how well the individual-level model fits the available data (Jusup et al., 2011) and independent validation of the physiological model (Jusup et al., 2014), there is nevertheless a lot of scatter that is in the current implementation simply ignored. PBT are renowned for roaming the Pacific Ocean, with an important migration route from western to eastern Pacific. The migration is undertaken by some juvenile fish who then spend considerable time along the coast of California (Block et al., 2011; Fujioka et al., 2018, 2015), and are likely to experience different conditions than juveniles who remain in the western Pacific. Taking such regional differences into account is possible by adding a migration component to the population model (e.g., as in Ijima



et al. (2015)). Our modeling framework, if equipped to handle regional differences, would be particularly well suited to assimilate data from archival tagging. Archival tags contain information on migration paths, seawater temperature experienced by the tuna, body length and maturation status at capture and recapture, and even an estimate of caloric intake (Aoki et al., 2017; Blank et al., 2007). Such information could be used to drive the physiological component of our modeling framework, providing both realistic environmental forcing for simulations, and independent data points to evaluate the performance of the simulations and improve the physiological model if necessary. We expect that such inclusion of environmental variability in the modeling framework would account for at least some of the scatter in PBT growth and reproduction data (Muller and Nisbet, 2000). More importantly, the inclusion would provide bioenergetic underpinnings to transpacific and spawning-related migrations, and help analyze effects of migration on ontogeny as a consequence of differences in environmental forcing.

Eco-evolutionary dynamics present another interesting venue for future research. Here, we have shown how maturation depends on environmental conditions, but natural environment may not be the only relevant factor. For the past six decades, PBT have been caught almost exclusively in the juvenile stage (Nakatsuka et al., 2017), which is fully consistent with our estimate that the survival probability from recruitment to the approximate age of sexual maturation is below 1 %, mostly due to fishing mortality. This kind of extreme selection pressure may have changed the population genetically and led to unexpected reproductive behavior (Wang et al., 2017). To predict changes in life history due to various selection pressures, the described modeling framework should be supplemented with compatible evolutionary equations. A first step in this direction has already been taken (Jusup et al., 2017b).

Finally, our results suggest that the survival of juveniles and young adults is the primary determinant of population growth at nearly all food abundances and temperatures under the current fishing pressure, and therefore should be the focal point of impactful fishing policies. In the context of such policies, one important difference between high and low food abundances is that high abundance makes older adults ( $>200$  cm FL) easily distinguishable in terms of size from younger adults (150–200 cm FL). This is a critical distinction for a size-based policy recommendation because older adults have already contributed considerably to population growth, while younger ones are yet to do so. The same distinction at low food abundance is impossible due to insufficient ingestion to support much growth in the adult stage. The applicability of size-based fishing policies may therefore change depending on environmental conditions.

Assuming current conditions and fishing pressure, we find that the relevant size below which fish should be protected is 200 cm fork length. If the environmental conditions were to change, the target size for protection would need to be recalculated. Because individual growth of PBT is more affected by changes in food abundance than realistic changes in temperature, special attention should be paid to changes in food abundance, which can be tracked either directly by monitoring prey populations, or indirectly by monitoring the nutritional status of caught tuna.

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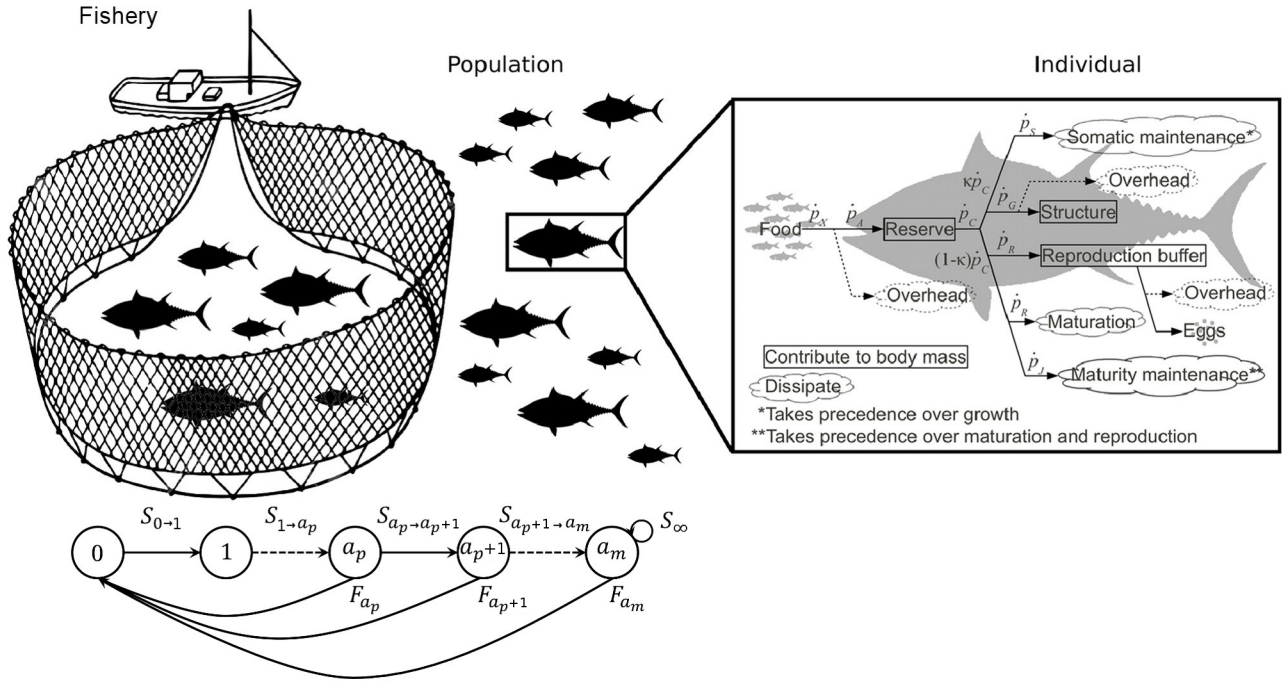
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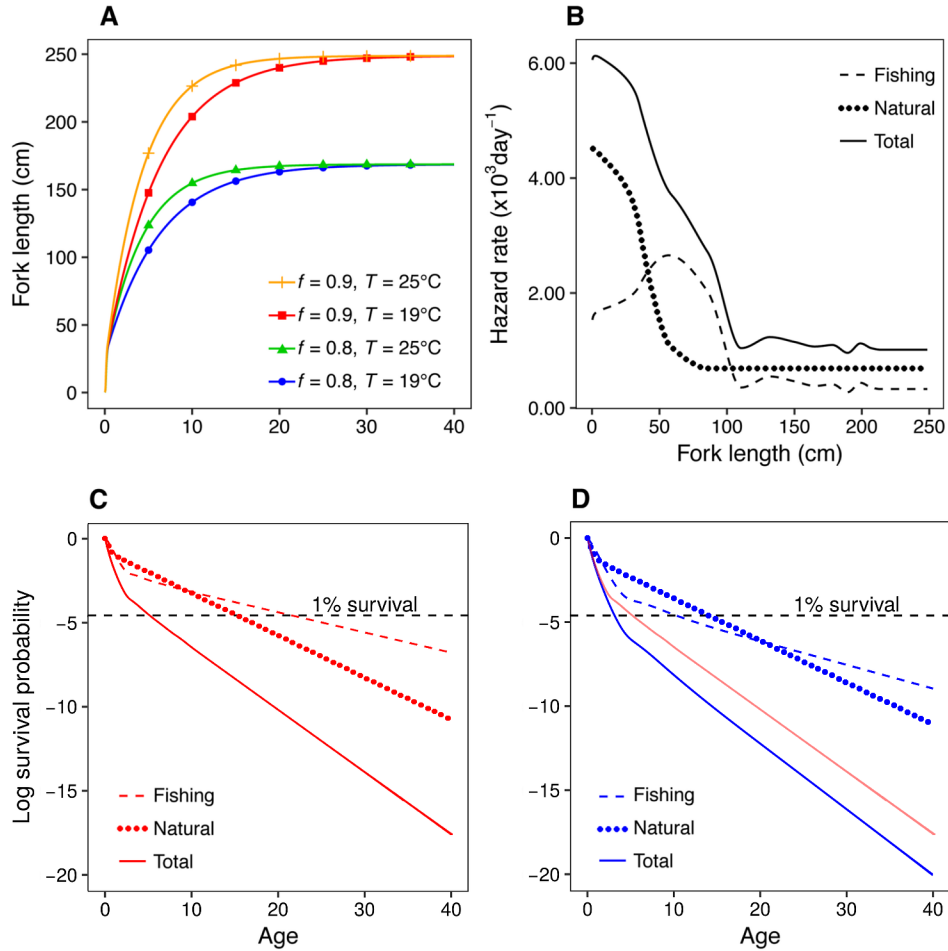
**Author Contributions** All authors contributed extensively to the work presented in this paper. H.I. and M.J. contributed equally.

**Author Information** The authors declare no competing interests, financial or otherwise. Correspondence should be addressed to H.I. (ijima@affrc.go.jp).

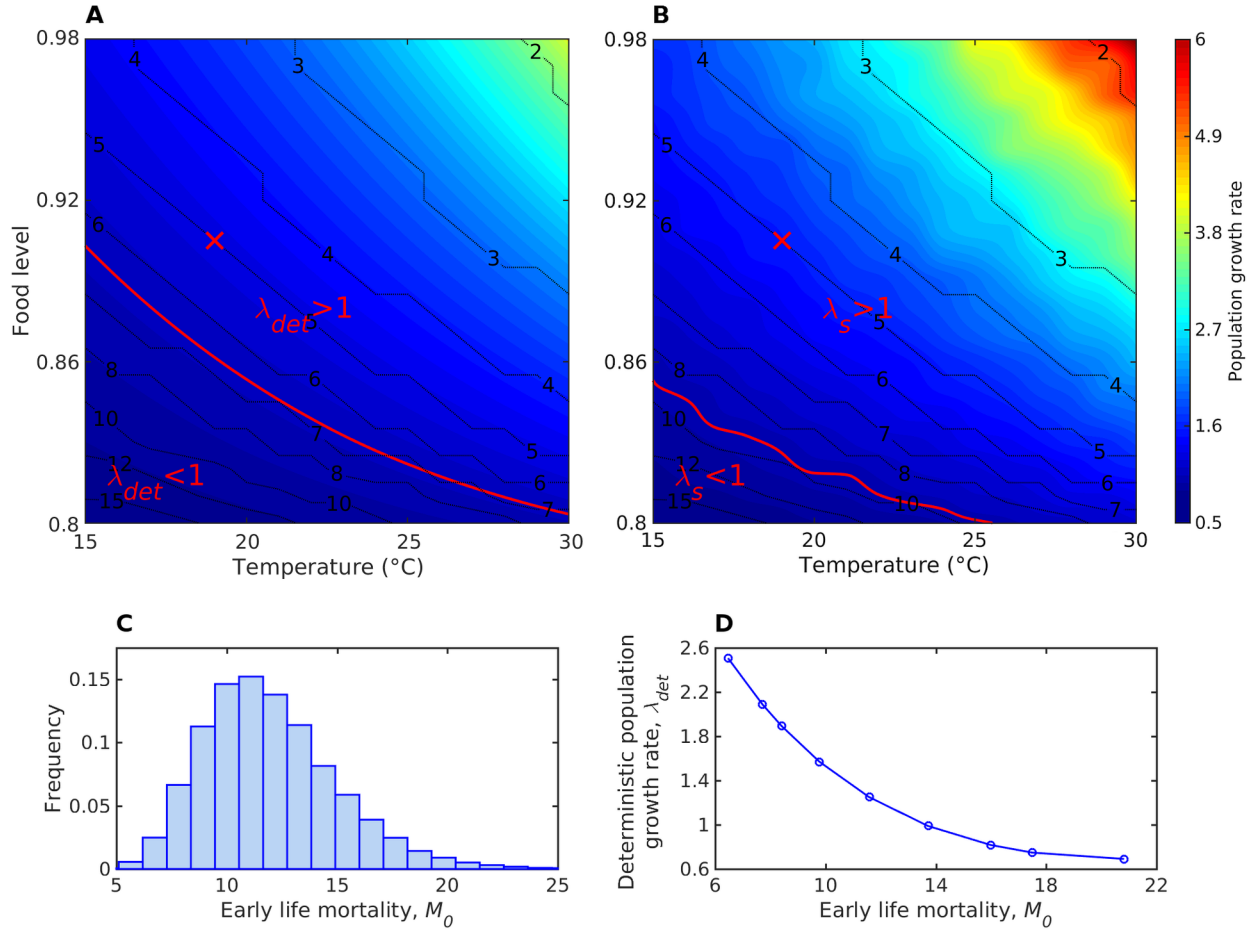
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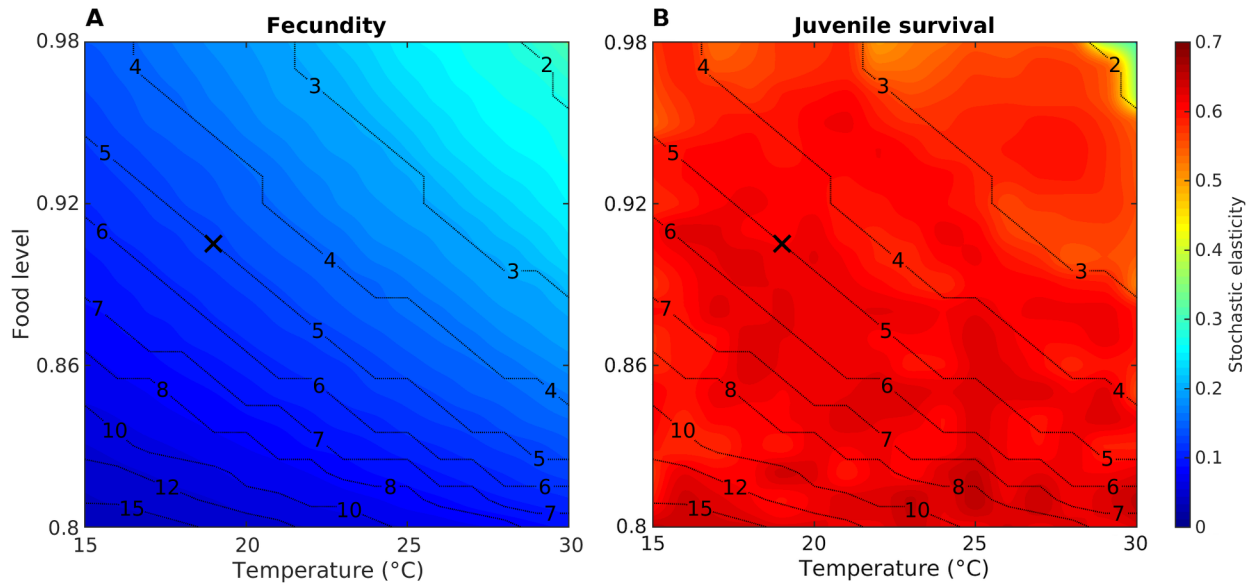
**Figure 1: Framework for capturing the effects of environmental changes and early-life stochasticity on Pacific bluefin tuna population growth under fishing pressure.** Individual-level ontogeny is obtained by—in contrast to statistical data fitting—zooming in on metabolic rates whereby growth, maturation, and reproduction become dependent on environmental conditions, e.g., food and temperature. The environmental dependences emerge at the population level as changes in the elements of the life-cycle graph: the age of sexual maturation,  $a_p$ ; fecundities,  $F_a$ ,  $a \in \{a_p, \dots, a_m\}$ ; and survival,  $S_{a \rightarrow a+1}$ ,  $a \in \{0, \dots, a_m - 1\}$  and  $S_\infty$ . Uncertain recruitment as the cause of early-life stochasticity is reflected in the random value of  $S_{0 \rightarrow 1}$ . In addition to natural causes of mortality, fishing effort is, due to its intensity, responsible for determining survival of practically all age groups.



**Figure 2: Growth, maturation, and survival of Pacific bluefin tuna depend on environmental conditions.** **A** PBT growth is dependent on both food and temperature. More food leads to higher ingestion relative to maintenance costs, thus inducing faster growth and maturation, as well as increasing the ultimate size. A warmer environment, by contrast, increases both ingestion and maintenance simultaneously, inducing faster growth and maturation, but leaving the ultimate size unchanged. **B** We assumed that the hazard rate due to natural and fishing mortalities is size-dependent rather than age-dependent. The reason for this assumption is the importance of size as an ecological variable; for example, vulnerability to a given predator or to a particular fishing gear depends on size. Hazard rate data are from ISC (2016). **C,D** Because growth depends on environmental conditions, while hazard rate depends on size, survival probability as a function of age changes with the environment. This needs to be taken into account when estimating the population growth rate. Note that high natural mortality of young juveniles (<40 cm fork length) is complemented with high fishing mortality (40–80 cm fork length), thus causing the survival probability to drop below 1% at the age of 5.15 (resp., 3.14) years in **C** (resp., **D**). Light red curve in **D** is the total survival copied from **C** for easy comparison.

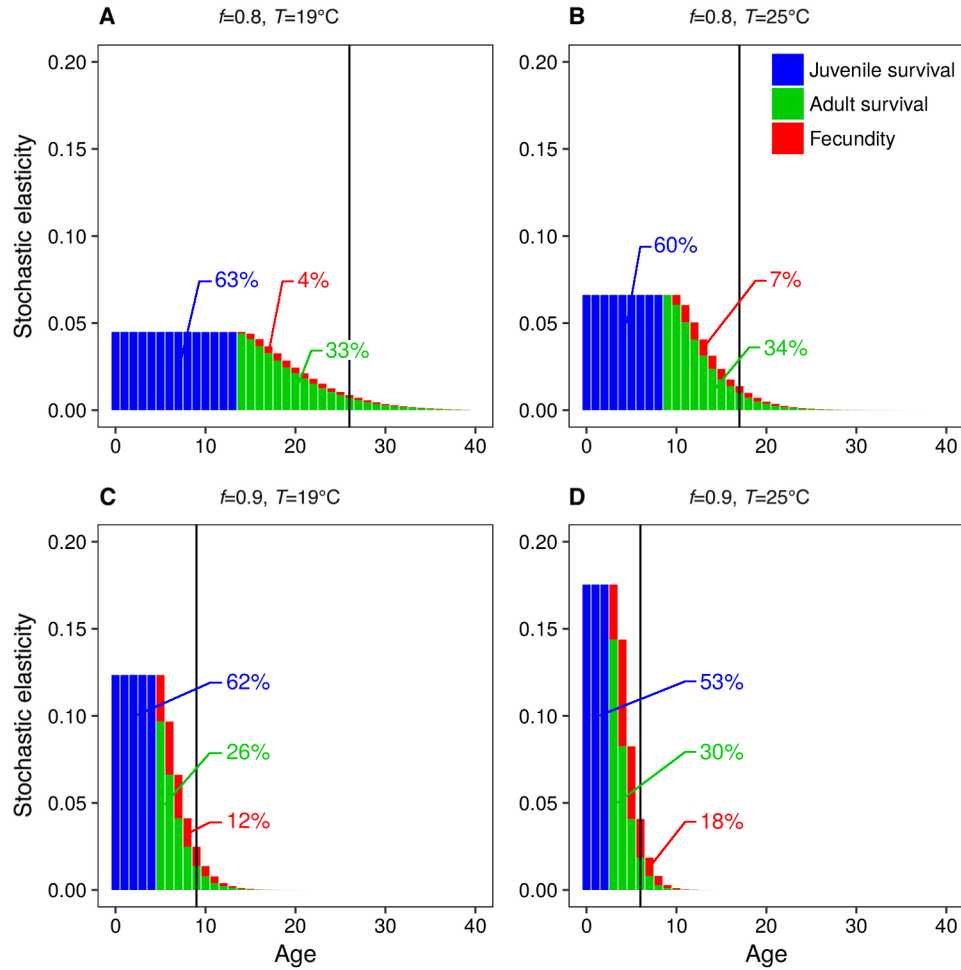


**Figure 3: Environment and early-life stochasticity strongly affect Pacific bluefin tuna population growth.** **A** Shown is the deterministic population growth rate of PBT as a function of temperature and food overlaid with sexual maturation age. An increase in both of these environmental variables positively affects tuna population growth, but the underlying mode of action is different. A higher temperature increases both energy assimilation and dissipation, thus providing more energy per unit of time without affecting the gap between sources and sinks. More food, by contrast, increases only assimilation, thus not only providing more energy per unit of time, but also widening the gap between energy sources and sinks. Environment strongly affects the sexual maturation age of PBT. As long as maturation age is 6-7 years old, population growth is positive. Red  $\times$  symbol marks the average conditions experienced by the present-day PBT (Jusup et al., 2011). **B** Stochastic population growth rate of PBT is considerably higher than its deterministic counterpart, pushing the maturation age boundary for positive population growth to 9-10 years old. **C** Distribution of early-life mortality due to Simon et al. (2012). Stochasticity in the early life history of tuna arises because an adult fish is capable of spawning millions of tiny ( $\approx 1$  mm in diameter) eggs whose survival is highly uncertain. **D** Faster population growth in a stochastic calculation than the corresponding deterministic calculation is a consequence of the convex, non-linear relationship between early-life mortality ( $M_0$ ) and population growth rate ( $\lambda$ ). Namely, Jensen's inequality applied to the function  $\lambda = \lambda(M_0)$  dictates  $\lambda_{det} = \lambda(\overline{M_0}) < \overline{\lambda(M_0)} = \lambda_s$ .



**Figure 4: Pacific bluefin tuna population growth is, given the current fishing pressure, much more responsive to changes in juvenile survival than changes in fecundity in almost all environments. A** 1 %-change in fecundity (i.e., the total reproductive output of an individual fish) contributes to <20 % of change in the population growth rate in all but the most favorable environments (upper right corner wherein this contribution reaches approximately 35 %). Black × symbol marks the average conditions experienced by the present-day PBT (Jusup et al., 2011). **B** 1 %-change in juvenile survival (i.e., from age 0 to sexual maturation) contributes to >50 % of change in the population growth rate in all but the most favorable environments (upper right corner wherein this contribution falls to approximately 35 %). A percentage change in population growth due to a 1 % change in an underlying vital rate such as fecundity or survival is called elasticity. Here we calculated stochastic elasticity because of stochasticity in the survival of Pacific bluefin tuna eggs and larva.





**Figure 5: Age beyond which individual fish contribute minimally to population growth is strongly dependent on environmental conditions.** In search of potential policy recommendations, we used stochastic elasticity to find age groups whose contribution to population growth is inconsequential under the present fishing effort. Juvenile survival, adult survival, and fecundity elasticity are marked in blue, green, and red color, respectively. Vertical lines separate age groups whose contribution to the total adult survival elasticity is  $<10\%$ . **A,B** Low food substantially prolongs the juvenile stage, thus emphasizing the importance of juvenile survival for population growth. If temperature is also low (**A**), fish in their late twenties or older barely contribute to population growth, while at a higher temperature (**B**), the same holds for fish in their late teens or older. In either case, however, the size of these “inconsequential” fish is almost indistinguishable from the size of young adults whose contribution to population growth is critical (see Fig. 2B). **C,D** Higher food abundance speeds up maturation sufficiently to make fish beyond age 10 unimportant for population growth. Here, the “inconsequential” fish (typically  $>200$  cm fork length) are easily distinguishable from young adults (150–200 cm fork length). Fishing policies based on size are therefore valid irrespective of the prevailing temperature, but may be impractical at low food abundances.